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MOLTING ADAPTATIONS OF ROCK PTARMIGAN ON AMCHITKA ISLAND, ALASKA

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ABSTRACT.—The molting pattern of Rock Ptarmigan (*Lagopus mutus gabrielsoni*) from Amchitka Island differs from that of other described races in the feathers molted, temporal and sexual sequence of molt, and extent of molt. Partially dark feathers may completely cover the head of females as a normal part of the winter plumage. Many new brown feathers or retained old ones are also found on the upper parts primarily of females but of both sexes in winter. To date, only the mid-summer and male autumn plumage, on which the description of this race was based, has been documented.

The Rock Ptarmigan (*Lagopus mutus*) has distinct races occurring on such islands as Newfoundland, Greenland, Iceland, Scotland, the Aleutians and Japan. Of the 13 Palearctic races recognized by Vaurie (1965), only one (*L. m. millaisi*) from Scotland is said to retain some brown feathers in winter (Vaurie 1965, Cramp and Simmons 1980). None of the 10 Nearctic races discussed in Ridgway and Friedmann (1946) is said to do this, although adequate descriptions of the winter plumage for the races *chamberlaini* (includes *sanfordi,* fide Gabrielson and Lincoln [1953]) and *gabrielsoni* were not available. Gabrielson and Lincoln (1959) accepted eight races for Alaska (one was newly described after Ridgway and Friedmann) for three of which, all Aleutian Island forms, winter plumages have not been described. In the original description of *L. m. gabrielsoni* from Amchitka, Aleutian Islands, Murie (1944) had only summer and autumn specimens but suggested that the winter plumage was almost certainly completely white.

At least two insular races of Willow Ptarmigan (*Lagopus lagopus scoticus, L. l. variegatus*) and the southernmost population of the race *L. l. maior* are known to retain brown feathers in winter (Vaurie 1965, Cramp and Simmons 1980). In addition, stocks of *L. mutus welchi* from Newfoundland have been transplanted to warmer climates (Salomonsen 1939), where they have been found to retain brown feathers in winter; in some populations, where winter conditions and snow prevail through the summer, white dorsal feathers are retained as a part of the summer plumage (Salomonsen 1939). It seems adaptive to retain those complements of feathers that will provide most security from predation in regions of variable snow cover or unique environmental conditions. Populations that retain such mixtures of feathers represent a departure from the "type" or "normal" molt pattern and sequence described by Salomonsen (1939). His "type" in the annual molt-activity of various feathers falls into five categories, some of which pertain to both sexes equally while others pertain to only one. These categories may be generally summarized as:

1. One molt (basic in autumn) per year (includes most large feathers and some under body feathers).

2. Two molts (basic plus alternate in winter) per year (mainly body feathers in males only).

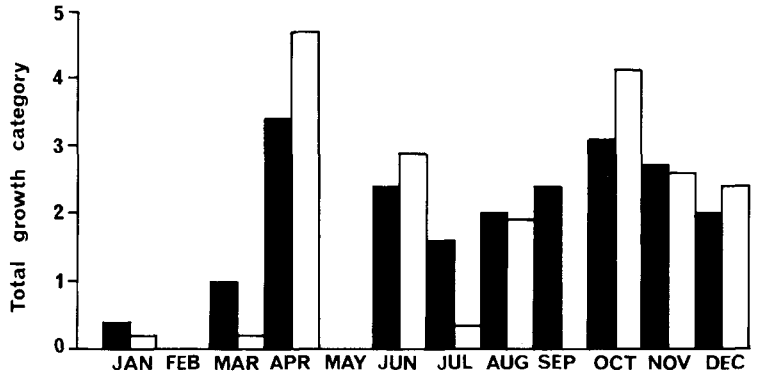
3. Two molts (basic plus supplemental in summer) per year (lesser wing coverts and under body feathers).

4. Two molts (alternate plus supplemental) per year (tertiaries in males, wing coverts in females).

5. Three molts (basic, alternate and supplemental) per year (upper parts, head, a few wing feathers and scapulars).

In addition to chronicling the sequence of molt in Rock Ptarmigan, Salomonsen (1939) speculated about the ecological functions of the molt, as well as the physiological and environmental variables affecting molting times, extent of molt, and coloration of plumage. Watson (1973) and Hewson (1973) presented data that raised doubt about some of Salomonsen's earlier hypotheses. Our findings also differ from the sequences that Salomonsen described.

While studying the avifauna of Amchitka Island, Alaska, we noticed that the winter plumage of the Rock Ptarmigan there, the southernmost Nearctic population except for Newfoundland, included many colored or partially colored feathers. We found that the par-



	JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC
♂	0.4	*	1.0	3.4	*	2.2	1.6	2.0	2.4	3.1	2.7	2.0
♀	0.2	0	0.2	4.7	*	2.9	0.3	1.9	*	4.1	2.6	2.4

FIGURE 1. Estimate of total growth of new feathers for each sex by month. The categories of growth used are: 0 = no growth, 1 = very light, 2 = light, 3 = moderate, 4 = heavy, 5 = very heavy (see text). Actual numerically summed scores are given by month on the numerical bar. Asterisks indicate no specimens.

tial brown coloration aided in concealing birds in areas of patchy snow that are so prevalent on lower portions of the Island in winter. Data from a study of skins taken at various stages of molt showed some interesting variations from the normal molting pattern generally accepted for Rock Ptarmigan as reported by Salomonsen.

METHODS

Sixty-nine specimens collected on Amchitka from 1969 to 1973 and five specimens from 1979 were preserved as flat skins. All months except May are represented; we had only six birds from August and September. An additional 13 specimens (mainly summer or winter birds) prepared as standard study skins were also available for parts of the study. The flat skins were studied and data collected by lifting the feathers carefully with forceps, noting the stage of growth, and estimating the progress of the molt. Separate estimates were given for each of the following areas: head, neck, back, throat, breast, wing, rectrices, upper tail coverts, under tail coverts and feet and legs. Total growth estimates (Fig. 1) were computed from the composite of all of the above areas. Visible plumage was given as a percentage of total area while growth was judged on a five-point scale where: 0 = no growth, 1 = very light growth, 2 = light growth, 3 = moderate growth, 4 = heavy growth, 5 = very heavy growth. Each increment represents approximately 20% of the incoming plumage being in a state of growth. Because the molt of the Amchitka ptarmigan differed from that in other subspecies, we could use Salomonsen's (1939) molting formula for the Rock Ptarmigan only with modifications that would render it meaningless for comparative purposes; therefore we did not use it. Further, while there are definite cycles of feather generation (sensu Palmer 1972) it was more difficult to fit these generations nicely into the Humphrey and Parkes (1959) scheme because of the protracted duration or overlap of some of the generations. We have, however, tried to use their terminology where we could readily do so and maintain the meaning of the process.

RESULTS AND DISCUSSION

PRESUPPLEMENTAL MOLT (WINTER TO SPRING)

The first feathers of the supplemental plumage appeared between mid-March and early April. Supplemental feathers appeared randomly on the head, neck, back, and throat. A characteristic of males in the 23 races studied by Salomonsen was a persistent period wherein the crown, occiput and ear coverts were brown while the remainder of the bird was white. This stage, according to Salomonsen (1939: 23) is "very characteristic . . . in all races" and "remains for a rather long time owing to the growth being very slight." *Lagopus m. gabrielsoni* showed uninterrupted and fairly concurrent growth of all supplemental upper body feathers. During this time, the upper tail coverts were so worn and because some were lost, the growing supplemental feathers beneath were exposed. When the upper tail coverts had nearly completed molt and the upper parts were 50% brown, summer feathers appeared on the wing.

As in other races, only the inner median upper wing coverts, innermost greater wing coverts, lesser wing coverts and tertiaries were molted, generally incompletely, at this time. Winter wing feathers were replaced slowly in a proximally directed wave. Females generally

retained fewer winter wing feathers and the molt was completed earlier than in males. The breast feathers were replaced rapidly in April, with the result that all males and most females were in complete summer dress by June. In June, the belly, which in males of all other races studied remained white during the summer, began, in both sexes, to grow dark summer feathers. In races mentioned by Salomonsen, males molted the belly feathers only once a year (autumn). Specimens of *gabrielsoni* taken in July showed extensive summer feather regeneration making up 40–60% of the belly feathers. The single male specimen from August had 100% summer belly plumage and the two September males (in the initial stages of the basic molt) also probably had 100% summer belly feathers in August (Fig. 1).

Males of races examined by Salomonsen (1939) molted the under tail coverts from summer to autumn and autumn to winter. In both sexes of *gabrielsoni,* the under tail coverts were molted from winter to summer as well as from summer to autumn. Summer growth occurred in mid-April, although one exceptional specimen from mid-April showed moderate growth of white feathers instead of brown. Eleven males from mid-June had 10–100% summer feathers. By the end of July, however, all birds had 100% summer plumage. September males had 100% summer under tail coverts with heavy autumn growth beneath. One male from October had 100% autumn under tail coverts. Growth stopped by October and white autumn feathers remained in all specimens until spring. Salomonsen also noted that females molted the under tail coverts three times yearly. As in males, female *gabrielsoni* molted this tract only twice yearly. The molt occurred more quickly in females than males, with summer feathers growing underneath the autumn plumage in mid-April and completely replacing it in all females by the first week of June. No evidence of growth was seen after the last week of June. Two birds from the middle and last thirds of August had 100% summer feathers with no new growth apparent. An October female, however, had 100% autumn feathers with very heavy autumn growth. The autumn feathers mostly completed their growth by the end of November (with the exception of one bird showing moderate growth in December) and no further growth or replacement occurred until spring.

The feathers of the legs and toes were also molted winter to summer rather than summer to autumn. Salomonsen (1939) pointed out that even in races with the most complete summer molt, under tail coverts and feathers of legs and toes are not molted until autumn.

Salomonsen reported a single molt of the central pair of greater upper tail coverts in males of all races he studied (summer to autumn). In *gabrielsoni* however, males molted these feathers twice yearly (as did females) from winter to summer as well as from summer to autumn.

Feather growth began around the first part of May and was complete by mid-June in females but not until late July in some males. In races studied by Salomonsen, but not in *gabrielsoni,* the throat feathers remain partially white throughout the summer. White throat feathers are completely replaced in April. Most males, however, retained a white chin through June and some until mid-July. Salomonsen stated that winter-to-summer molts of males and females occurred simultaneously. Watson (1973) and Hewson (1973) refuted this with data from observations of the Scottish ptarmigan (*millaisi*), finding that males preceded females. Watson (1973: 207) noted that this finding "might question his [Salomonsen's] explanations of the hormone mechanism underlying these . . . molts and other ideas about the evolutionary origin and current function of these molts." In *gabrielsoni* also, males were ahead of females until around mid-April. Values for March feather growth were 1.28 for males and 0.28 for females (see Fig. 1). Females concluded the molt sooner than males and all birds concluded their summer growth by the first week of August.

DEFINITIVE PREBASIC MOLT

The prebasic molt of the primary remiges commenced in late July or early August in males and about two weeks later in females (Fig. 2). Primaries were molted from the innermost to the outermost, usually with no more than two or three growing at a time. Growth was completed in both sexes by mid-October. At the same time in males, feathers molted rapidly over the back, neck, head, throat, breast, and tail, their basic (autumn) replacements finishing the growth by the end of August. Females molted these feathers about two weeks later than males, and proceeded with equal rapidity and completeness. The remaining feathers of the wing were molted during the basic primary molt, beginning during the growth of the fourth or fifth primary. Males showed no growth of wing feathers after August while females still had heavy autumn growth in late October. Prebasic molt on the belly began during September in both sexes and was completed in females by the end of October, but in a few males not until the end of November. One male retained about 5% supplemental (summer) feathers through December. The prebasic molt of under tail coverts began in August in both sexes;

it was complete by October in males but continued until December in females.

Replacement of upper tail coverts also began in August and the molt was prolonged in both sexes, still extensive in December. Although the molt of these and some before-mentioned feathers completely overlaps the prealternate (winter) molt of other feathers, we consider it part of the prebasic molt. Because these feathers began growing early in the autumn and were not shed until spring, they must be recognized as belonging to the total basic (autumn) plumage. The feet and legs began to replace feathers lost during the summer in September. In *gabrielsoni* the first basic feathers appeared early in August and the molt was completed by mid-October (except for some tail coverts).

Salomonsen indicated (1939: 38) that as a rule a variable number of summer feathers are retained through the autumn, especially in more northern races. We did not see this suppression of the prebasic molt in *gabrielsoni*. Although females were preceded by males, as is typical, the females molted completely into basic plumage.

ALTERNATE (WINTER) PLUMAGE

The prealternate molt replaced only part of the basic plumage. It overlapped the prebasic molt because some basic feathers were still growing when the prealternate molt was nearly complete. The prealternate molt replaced feathers on head, neck, back, throat, breast, and the same wing coverts and tertiaries that were molted in spring. Feathers on the breast and throat of birds of both sexes and the innermost upper wing coverts in males, began molting in early or mid-September. They grew very slowly and did not complete growth until the end of December. About 5% of basic feathers were retained through the winter on the breast and belly of a few birds. Feathers on the upper parts began their prealternate (winter) molt in mid-October. They too grew slowly, continuing until the end of December although some specimens show growth in January and one even in February. This slow growth gave the birds a mottled appearance through November and December that appears to camouflage them in patchy snow cover. We observed that when birds were flushed at this season, they would most often alight on snow-free ground at the edge of a snow patch rather than on the snow or away from the snow patch.

On females, the innermost upper wing feathers began molting in late October or early November, much later than in males owing to the delayed prebasic molt in females. Feathers of the alternate plumage began appearing im-

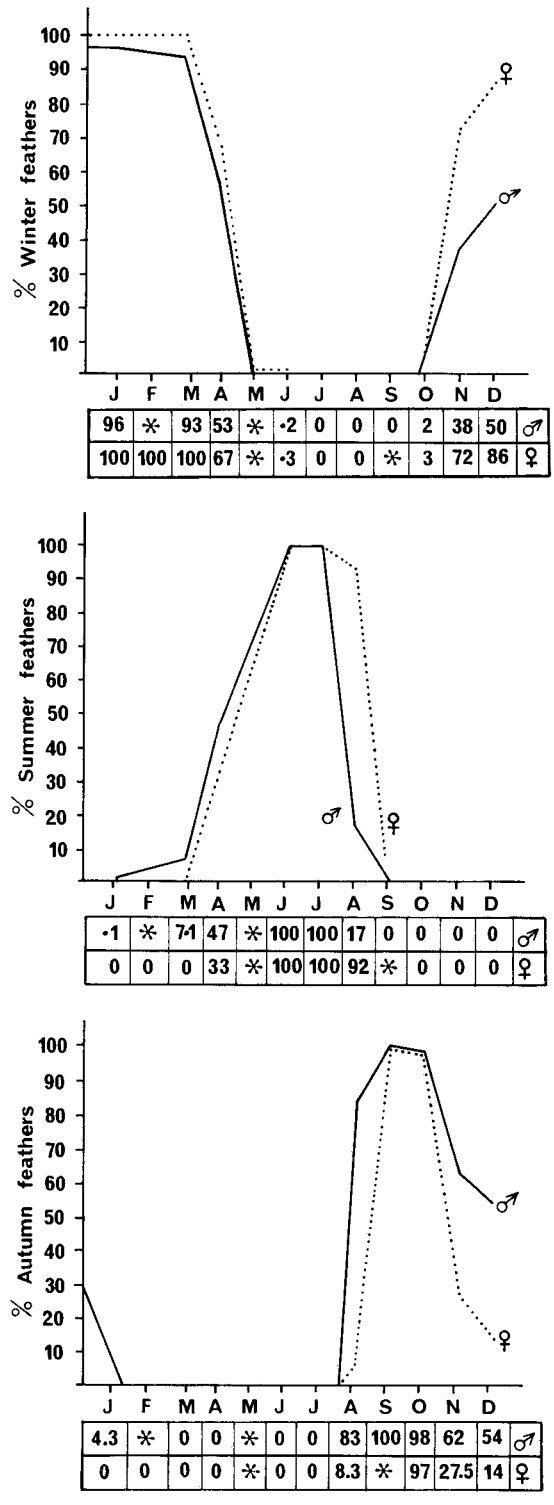


FIGURE 2. Comparisons of amount of visible new plumage on head, neck and back for winter, summer, and autumn feathers by sex. Actual percentages are given by month on the numerical bar. Asterisks indicate no specimens.

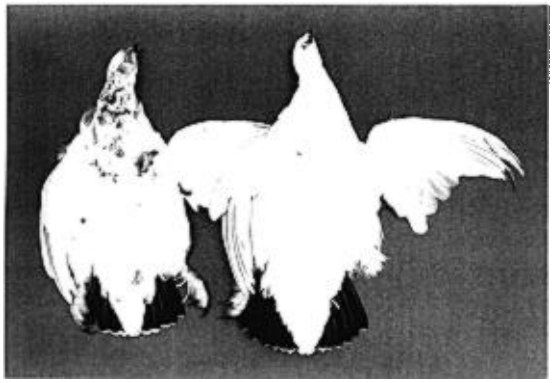


FIGURE 3. Comparison of average female (left) and male (right) Rock Ptarmigan in alternate (winter) plumage. Both specimens taken 15 January 1970, Amchitka Island, Alaska.

FIGURE 4. New-growth, brown, alternate (winter) feather showing white tip and brown base. The tip makes up about 7 mm of this dorsal feather. Feather taken from a December specimen.

mediately after the basic plumage was complete, and the alternate plumage was usually complete by the end of December.

Both male and female birds from Scotland to the high Arctic, were said by Salomonsen (1939), to complete the molt from autumn to winter plumage (i.e., prebasic molt) at the same time. Watson (1973), however, found that females of *L. m. millaisi* completed the molt before males. We found the same in *L. m. gabrielsoni* (although ultimately males were whiter than females, due to the brown feathers associated with the female alternate plumage).

Rock Ptarmigan on Amchitka bore brown or partially brown feathers during the winter (Fig. 3). The alternate plumage was previously assumed (Murie 1944) to be completely white (except for the rectrices and the male loreal stripe). Brown feathers have been described in the normal alternate plumage of at least two other races, *L. m. millaisi* and *L. m. welchii* (from Newfoundland). In addition, Salomonsen (1939) reported rare brown feathers of various origins in the alternate plumages of most races. M. Ralph Browning (pers. comm.) informed us that all the U.S. National Museum of Natural History specimens collected in January and February have at least some brown feathers. Watson (1973: 210–211) noted that "white feathers with dark tips and bases occasionally grew on the breast or upper parts at the same time as adjoining pure white feathers." The same is true in *gabrielsoni* (Fig. 4).

In Scottish ptarmigan, males have a greater percentage of brown feathers than do females (39% in November males compared to 9% November females, and 19% January males compared to 6% January females; Watson 1973, Hewson 1973). We found that the prealternate molt began in *L. m. gabrielsoni* somewhat later than in *L. m. millaisi* and was normally completed by the end of December in females and the end of January in males. Some males retained a few basic feathers on head and neck, which never comprised more than 5–10% of the dorsal plumage. A few (2–5%) new brown alternate feathers grew on the back in about 30% of the males. Females did not retain basic feathers but either grew white-tipped black or brown alternate feathers (or grew both) over the entire head and nape, as well as many new feathers that were partially or totally brown scattered over the upper back. The alternate feathers of the head, nape, and back of males were entirely white.

COMPARISON OF *L. M. GABRIELSONI* TO *L. M. MILLAISI*

Of all the races described by Salomonsen (1939), *millaisi* is the closest to *gabrielsoni* in most molt adaptations and in the environment where it occurs, yet some significant differences exist. Although summer temperatures are higher in Scotland, *millaisi* begins the prebasic molt as early as June, while *gabrielsoni* begins it one or two months later. Extending the supplemental (summer) plumage in *gabrielsoni* allows white belly feathers to be replaced with brown ones, and the legs and feet to molt completely as part of the presupplemental molt. The basic plumage is retained longer in *millaisi* than in *gabrielsoni*. The prealternate molt starts slightly later in *gabrielsoni* than in *millaisi*. Like Scottish birds, *gabrielsoni* showed a com-

plete basic plumage in October. This, Salomonsen explained (1939: 103) is "exceptional to all other populations." The two races differ markedly, however, in the duration of the autumn molt. The Scottish ptarmigan begin molting primaries early in June and the molt is completed by the end of September (Watson 1973). Both races differ from Salomonsen's "type" in that females precede males into alternate (winter) plumage. Both races retain old and grow new brown feathers as part of the alternate plumage, yet in *millaisi* the brown feathers are much more prevalent in males while in *gabrielsoni* they occur mostly in females. In *millaisi* the presupplemental molt often overlaps the winter molt, perhaps in relation to the relatively high winter temperatures. Such overlapping does not occur in *gabrielsoni,* and brown feathers that grow as part of the alternate plumage in females are not related to summer growth. Both *millaisi* and *gabrielsoni* again differ from Salomonsen's "type" as males precede females into supplemental plumage. Since Amchitka and Scotland have similar climates, we cannot readily explain the differences in the molt schedules of their ptarmigan.

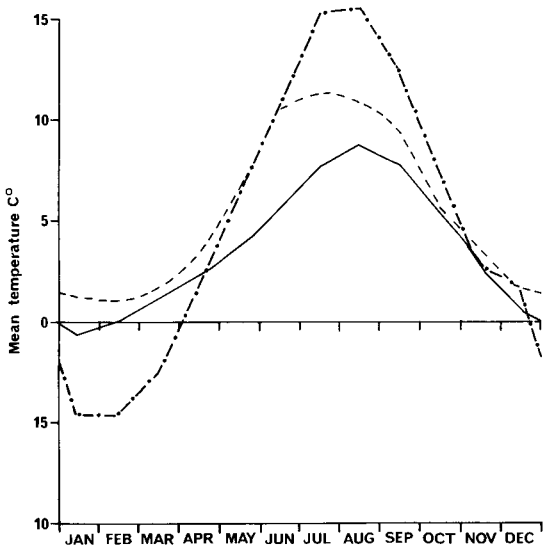


FIGURE 5. Comparison of mean temperature at three island localities where Rock Ptarmigan have variable amounts of brown alternate (winter) plumage. Solid line = Amchitka (Armstrong 1977), dot-dash = Scotland (Salomonsen 1939), dashes = Newfoundland (Salomonsen 1939).

COMPARISON OF ALEUTIAN ROCK PTARMIGAN

Six other subspecies of Rock Ptarmigan live on islands of the Aleutian chain (*evermanni, townsendi, chamberlaini, atkhensis, yunaskensis, nelsoni*), each occurring on groups of two to three major islands. More than 240 km of latitude separate the northernmost from the southernmost (central) islands in the chain. The weather may differ markedly between a northern island of great physiographic relief (e.g., Attu) and a southern island of low, relatively uniform relief (e.g., Amchitka). In May, for example, Attu is still in winter conditions while Amchitka has normally already been snow-free for two months. The persistence of snow on various islands, or its uniform presence during winter, seemingly occurs because of the islands' physiography. When the ptarmigan on each island group are better known, certain predictions about winter plumage may be possible, based on island size in relation to latitude and physiography (mean elevation, relief, etc.). We suspect that other southern races, such as *townsendi* from Kiska and *chamberlaini* from Tanaga and Kanaga (but perhaps not Adak), which have poorly known winter plumages and are adjacent to *gabrielsoni,* share some of the characteristics of that race. The presumed differences first suggested for *sanfordi* (from the low, flat island of Kanaga but now in synonymy with *chamberlaini*) and *chamberlaini* (from Adak with its larger size and great relief) may be explained by climatic conditions. A study of their molts and comparison with our findings would perhaps disclose trends in southern or island populations and help elucidate the evolution, ecology and mechanism of ptarmigan molt.

CONCLUSIONS

Our study of molting in Rock Ptarmigan revealed several differences between Amchitka birds and other subspecies. These differences are likely due to the conditions on a small wind- and rain-swept ocean island where snow cover can vary from none in the lowlands to total within one week in mid-winter (Armstrong 1977; pers. observ.). Temperature is undoubtedly a factor in molting although some subspecies of Rock Ptarmigan, particularly *millaisi,* that are subject to higher yearly temperatures (Fig. 5) differ less than *gabrielsoni* from Salomonsen's "type." Briefly, the distinctive features in the molting of *L. m. gabrielsoni* are: In the presupplemental molt, summer feathers appear randomly over the upper parts and throat, and there is a delayed period when only the head is brown. Males develop brown supplemental belly feathers although they do so later than females. Under tail coverts are molted in the prebasic and presupplemental molts of both sexes. In other races, females molt these feathers in all three molts and males in the prebasic and prealternate molts. Feathers of the legs and toes are

replaced in the presupplemental molt, rather than the prebasic molt as in other races. The central pair of greater upper tail coverts are molted twice yearly (prebasic and presupplemental molts), rather than once a year (prebasic) as in, especially males of, other races. White throat feathers are not generally retained during the summer. Males preceded females in the spring although males completed the presupplemental molt sooner. Female prebasic molt was not suppressed as reported in other races and *L. m. gabrielsoni* like *millaisi,* displayed a complete basic plumage in October. Alternate feather growth was slow and the ptarmigan, especially males, had a mottled appearance through December. Females completed the alternate molt before males. Females grew many colored feathers as part of their alternate plumage. Males retained a few basic feathers through the winter but grew mostly white alternate feathers.

Watson (1973) thought that ptarmigan at lower elevations had more brown feathers in winter than those at higher elevations. We do not have an adequate sample from upland Amchitka (elevation 355 m), which remains largely snow-covered during winter, but our impression is that a larger percent of the ptarmigan there were completely white. Year-old or older males were uncommon during winter in the lowland and we presume that they were in the uplands. By spring older males again appeared in the lowlands (White et al. 1977). An initial partitioning of the habitat by sex (upland vs. lowland) may have been one factor leading to the greater amount of brown alternate feathers in females than males during winter.

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